COD AND HYDROGRAPHY
A REVIEW

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COD AND HYDROGRAPHY - A REVIEW

by

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ABSTRACT

The effect of hydrographic conditions on various parts of the life cycle of the cod has often been described in the literature. This paper is an attempt to correlate many reports and to compare them one with another.

Cod and Hydrography - A Review

by

John P. Wise

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COD AND HYDROGRAPHY

A Review

Scattered through the literature of fishery science is much information on the relation between cod and hydrographic conditions where they live. In some instances, notably the water temperatures frequented by cod of marketable sizes, there are many papers on the specific relationship. But often only the results of single experiments or isolated observations have been reported.

This paper is an attempt to organize and summarize the information available, both in the longer works and in the scattered bits of data. It is without doubt incomplete, but may perhaps serve as a starting point for the conducting of experiments or the making of observations. It may prove useful in helping the researcher who is not completely familiar with the literature to interpret observations made by himself or others.

All papers quoted have been read by the author, with one or two exceptions where sources that seemed too important to omit were unavailable. These exceptional instances are noted in the bibliography along with the secondary source from which the information was actually derived.

For the sake of uniformity and to accord with modern practice, temperatures have been rendered in the Centigrade system. Where conversion from Fahrenheit has been necessary, the calculation has been carried to the first decimal place; otherwise temperatures are quoted as given in the original. If the temperatures are given in whole degrees they are so stated without the addition of a decimal point and zero or zeroes. If the paper cited gives temperatures to the nearest tenth or hundredth degree, they are so quoted. This makes for an appearance of inconsistency, particularly in tables, but so long as different systems of mensuration prevail, inconsistency is inevitable.

Salinities are handled similarly, quoted exactly as given, except when they have been expressed in units of specific gravity or density. These latter have been converted to salinities in parts per thousand ($^{o}/oo$) by the use of Knudsen's Tables (Knudsen 1901) to the nearest hundredth of a part per thousand by weight of salt. In one or two older papers, salinities have been cited in percent; these have been changed by moving the decimal point.

As a convenient method of handling the information and relating hydrography to the cod, the various phases in the biology of the fish are taken up in turn. Under each segment of the life history the appropriate hydrographic phenomena are considered.

SPAWNING

Temperature

Authorities agree that the spawning of cod is influenced by temperature. Tåning has described on more than one occasion (1949, 1953) a warming trend in West Greenland waters during recent years which has been associated with an increase of spawning in that area, and Thompson (1943) mentions that in eastern Canada the cod spawn earlier in the year in areas where the water is warmer.

Fridriksson (1949) recounts a change in spawning habits at Iceland--from the earliest recorded times until the 1920's cod spawned only off the south and southwest coasts, moving to the colder waters of the northeast and east coasts after spawning season. However, in the early 1930's cod were found spawning all around Iceland as the waters became warmer. One effect of temperature on spawning, and indirectly on the fishery in this case, was that yield declined even though the numbers of fish probably increased, because the fish were more dispersed during the spawning season.

The consideration that temperature per se at spawning time may not be the critical factor for spawning success has been advanced by Eggvin (1934), Sund (1936), Poulsen (1944), and Heegaard (1947). Heegaard and Sund agree that spawning in some areas coincides with great variation in temperature in the water column, and contend that it actually takes place in the

discontinuity layer. Poulsen observes that cold temperatures in the months preceding spawning may have considerable effect in delaying the maturation of the gonads, and A. Dannevig's (1947) conclusions concerning the 1938 year class in the Transition Area agree.

Various theories about preferred and optimum temperatures have been advanced without supporting evidence. Damas (1909) states that European cod spawn at temperatures from 2° to 6° and that the optimum is probably above 4°. An American opinion (Anonymous 1932b) is that cod on our coasts prefer temperatures between 3° and 5°, and that they gather ready to spawn at about 2.5°.

A few instances of captive cod spawning in tanks or live cars have been recorded, and these cite temperatures from as low as -1.1° (Bigelow and Schroeder 1953), to a range of 0° to 5° (A. Dannevig 1919), to voluntary spawning at 5.5° (Anonymous 1911).

On the American side of the Atlantic, in the ocean, spawning temperatures are reported variously as from 0.6° to 8.9° (Bigelow and Schroeder 1953), 0.56° to 10.1° (Fish 1929), 8° to 12° (Tremblay 1942), and 7° to 12° (McKenzie 1934b). It should be understood that some of these authors were describing individual groups of fish and do not claim that these are spawning ranges for all cod in the Northwest Atlantic.

Schmidt (1926) reports little or no spawning at Iceland below 6°. Spawning at 6° is recorded for one year on the Norwegian coast and in the fjords by Hjort and Petersen (1905), although they mention that this was an exceptionally warm year. Sund (1935) describes cod seen in pelagic spawning concentrations on echosounding traces at Lofoten from 3° to 6.5°.

In the Barents Sea the maximum accumulation of cod eggs at the surface is found in areas where the bottom temperatures are 0° to 2°, although Rass (1936) considers the possibility of pelagic spawning in upper layers where a more moderate 3° to 4° is found. He speculates that the difference between the spawning temperatures off the Murman coast and those along the Norwegian coast (see above) may be a possible indication of a racial difference in the stocks of cod.

Poulsen (1931) describes spawning in Danish inner waters where the preferred temperature seems to be 3° to 7°, although extremes of 2° and 8° have been observed.

To sum up, actual observations of cod spawning in captivity prove that temperatures from -1.1° to 5.5° are physiologically possible. Indirect evidence from distribution of eggs on the surface, concentrations of fish in the spawning season, etc., indicate a range of from 0.6° to 12° in the Northwest Atlantic, and from about 0° to 6.5° in the Northeast Atlantic, with the extremes of all observations being from -1.1° to 12°. There is some evidence that cod will leave the bottom and school pelagically to spawn at a suitable temperature. Not to be neglected is the idea of some Scandinavian workers that variation in temperature in the water column rather than temperature per se may be the determining factor.

Salinity, oxygen and pH

Damas (1909) states that cod on European coasts spawn at about 34°/oo - 35°/oo salinity, while Bigelow and Schroeder (1953) think it is probable that no American cod spawns at less than about 32°/oo nor more than 32.8°/oo, giving a figure of about 32°/oo for Georges Bank. Damas, however, cites 35.16°/oo for the Grand Bank. One anonymous source (1932b) says that cod "prefer" 33°/oo to 34°/oo on American coasts. In general we may agree with Bigelow and Schroeder that American cod spawn at lower salinities than do European, with the exception of Baltic cod, which spawn at about half the usual oceanic salinity. Whether the matter of salinity at spawning time is strictly coincidence or whether salinities may induce or delay spawning seems to be an unanswered question.

Sund (1935) cites an instance in which cod were found spawning pelagically in layers of water which had appreciably lower concentrations of oxygen and lower pH than the adjoining layers above and below, but gives no values.

EGGS AND LARVAE

Temperature

A relation between temperature of

the water during the pelagic egg and young stages of the cod and the later yield of the year class has often been described from different areas. In Danish waters, Blegvad (1926) notes that higher temperatures during the time when the eggs and larvae are pelagic is associated with higher year class yields. This is confirmed by Jensen (1952a). Similar findings are reported by Hermann (1951, 1953) for West Greenland, and Frost (1938) for Newfoundland. On the other hand, A. Dannevig (1947) says that the successful 1938 year class in the Transition Area is associated with cooler water temperatures than usual, the rationale being that spawning was delayed and the larval period corresponded better with the height of the zooplankton cycle. Poulsen (1931), however, states that the higher the temperature in Danish waters, the more larvae he found, and concludes that this is a reflection of the availability of planktonic food.

A close association between the temperature on Fylla Bank off West Greenland and the later yield of the appropriate year class has been reported (Hermann 1953; Hachey, Hermann and Baily 1954). Here again warmer years have produced better year classes (fig. 1).

Jensen (1929) found a similar relationship for Schultz' Ground in the Baltic,

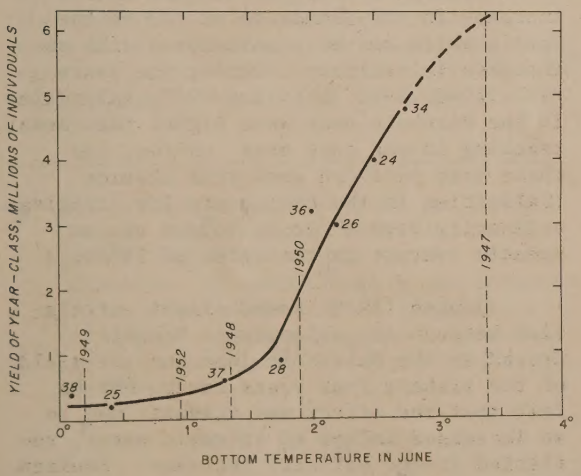

Figure 1.—Relation between the temperature on Fylla Bank and the yield of year classes of cod. (Redrawn from Hachey, Hermann and Bailey 1954.) Temperatures of recent years are marked by dotted lines.

and Poulsen (1930) observed that the number of larvae at Halskov Rev in the Belt and Anholt Knob in the Kattegat increase as the temperature increases when he compared several years data, although he suspects that the effect may be a secondary one, due to the increased availability of plankton as food for the larval fish in warmer years.

Many laboratory experiments and direct observations of the relations between eggs and temperatures have been made. Fertilization can take place as low as -2° (A. Dannevig 1919) and probably at least up to the highest spawning temperatures recorded, 12° (McKenzie 1934b, Tremblay 1942). Observations have shown that eggs are fertilized at 5.5° (Anonymous 1911) and as low as -1.7° (Johansen and Krogh 1914), but eggs fertilized at low extremes and kept at these temperatures are unlikely to survive. Hensen (1884) says that eggs die below -1.2°, and Johansen and Krogh (1914) report little or no development in eggs kept in temperatures up to -1.2°, with only incomplete development up to -0.3°. They conclude that the lower limit for full development lies somewhere between -1° and 0°. These conclusions, however, are not entirely consistent with the results of experiments described below.

The reports by Earll (1880) and H. Dannevig (1895) seem to be the classics in the study of time, temperature, and development of cod eggs. (Table 1.)

The results of the two experiments agree very well with the exception of the long periods at temperature below 0°. Even this is not particularly disturbing when it is considered that H. Dannevig's is an extrapolated rather than observed figure and that H. Dannevig himself comments on the variable results obtained in this sort of experiment. The temperatures given by Brice (1897) agree also, and those cited by Hensen (1884) and Ryder (1886) differ but little.

Thompson (1943) is not specific about temperatures for developing eggs, but he infers that above 5° is optimum, agreeing with Brice (1897), who adds a top limit of 8.3°. Johansen and Krogh (1914) have deduced that cod eggs in the Baltic routinely develop between 1° and 4°, and conclude incidentally that Van't Hoff's theory that a rise of 10° doubles the speed of chemical

Table 1.--Earll's (1880) and H. Dannevig's (1895) time-temperatures for the development of cod eggs.

Temperature (°C)	Time for development (in days)	Author
-1°	42	Dannevig
-0.6°	50	Earll
0.6°	34	Earll
1.1°	31	Earll
2.2°	24	Earll
3°	23	Dannevig
3.3°	20	Earll
4°	20.5	Dannevig
5°	17.5	Dannevig
5.0°	16	Earll
6°	15.5	Dannevig
7.2°	13	Earll
8°	12.7	Dannevig
10°	10.5	Dannevig
12°	9.7[1]	Dannevig
14°	8.5	Dannevig

[1] Reported elsewhere in the same paper as 9.3 days.

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reactions cannot be shown to apply to developing cod eggs.

Bonnet (1939) found that temperatures above 13° were invariably fatal to cod eggs (contrary to H. Dannevig above), and claimed in addition an increasing mortality from temperatures of 6° up, although Jacobsen and Johansen (1908) performed in their experiments on the specific gravity of cod eggs at temperatures from 12° to 20°. A. Dannevig (1919) also hatched eggs up to 14°, but concluded that the optimum is in the neighborhood of 3° to 5°. Another opinion of the optimum temperature is 2° to 8° (Anonymous 1932a). Bigelow and Schroeder (1953) place the optimum between 5° and 8.3°. Rognerud (1889) found that eggs hatched in 5° produced strong and vigorous larvae, but those hatched at 2.5° and 7.5° did not.

Schmidt (1931) concluded that the temperature of development has a definite effect on the meristic characters of cod, that the number of vertebrae and fin rays increases as the temperature decreases.

Lethal and optimum temperatures for fry differ from those for eggs. Here again there are field observations such as those made by Schmidt (1926) when he found no fry in Icelandic waters below 4° and by Hjort and Petersen (1905), who found them in temperatures over 5° in Norway; Johnstone (1906) notes that young cod, perhaps beyond the fry stage, are found in the North Sea in temperatures of 6° to 7°. Tåning (1953) states that temperatures below about 1.8° are lethal. Optimum temperature has been stated as 7° to 9° (Anonymous 1932b), although A. Dannevig and Sivertsen (1933) observe that fry survival up to 16° in laboratory jars.

In summary then, the maximum range for the development of cod eggs to the hatching stage is from -1° to 14°, but various authorities agree for the most part that the optimum is within a few degrees on either side of 5°. Larvae, on the other hand, can survive a range of similar magnitude but slightly higher, from about 2° to 16°, with an optimum of perhaps 7°. These values are as might be expected for a fish which is for the most part a late winter and early spring spawner. It would be interesting to experiment with the eggs and larvae of one of the few groups of cod known to spawn in the autumn to see if the lethal and optimum temperatures vary. It is difficult to see how the fry survive the winter unless there is a marked difference in temperature tolerance.

Salinity

Alander (1952) describes a recent increase in the abundance of cod in the Baltic which has been associated with an increase in salinity. During the years 1937, 1940, 1942, 1943 and 1947, salinities in the Bornholm Deep were higher than usual, reaching in one case over 18°/oo, and these have produced good year classes. (Salinities in the Baltic are low, ranging ordinarily from 4°/oo to 16°/oo vs. an oceanic average on the order of 35°/oo.)

Jensen (1929) found slight correlation between the salinity at Schultz' Ground in the Baltic in June and the yield of the fishery four years later, but he felt that the effect was actually due to an increased inflow of Atlantic water, reflected in the salinity increase. Poulsen (1944) suggests that this influx and the associated salinity change may influence the migration of mature fish.

Poulsen (1930) detected little agreement between the salinity in the Belt and Kattegat in February-May and the number of cod larvae, but rather high agreement between the bottom salinity in November-January and the numbers of fry in the following spring. This supports Jensen's (1929) hypothesis that increased inflow of Atlantic water, which may be diagnosed by a salinity increase, is responsible for good year classes rather than salinity per se.

Schmidt (1931) was unable to demonstrate any connection between variation in meristic counts and salinity differential, as he had found for temperature.

Perhaps the most important effect of salinity on the eggs and nearly helpless larvae and fry of the cod is in the changes of density of the water which may cause the planktonic forms to float on the surface, suspend at some intermediate layer, or sink to the bottom. Bigelow and Schroeder (1953) note that in wet springs runoff from the land may dilute the surface of the sea so that eggs are suspended in intermediate layers, while A. Dannevig (1947) points out that in years when winds keep brackish surface waters offshore the eggs can float higher and get more light, which he feels is conducive to hatching.

An example of the suspension of eggs below the surface is given by Dahl (1909), who reports that at one station in the Kattegat (for instance) he found very few eggs or larvae at the surface in 6.32°/oo 1/, and the great majority at 30 meters in 29.16°/oo.

1/ Dahl (1909) as quoted here and below states salinities as densities in σ_t units, which are usually taken to mean densities at temperature t, uncorrected to standard densities at temperature 0° (σ_0). However, since he mentions no temperatures and in a footnote defines:

$$\sigma_t = (\text{Albs. sp. gr.} - 1)\ 1000,$$

which in modern usage is more usually represented as σ_0, his σ_t has been taken as σ_0 in converting to salinities.

Dahl (1909) and A. Dannevig (1919) conducted laboratory experiments, observing eggs and larvae in waters of different salinities. While the two experiments were designed for somewhat different purposes, Dahl's to determine what salinities were necessary to float eggs and larvae, and A. Dannevig's to investigate moraality caused by salinity, the results are comparable.

Table 2.--Dahl's (1909) and A. Dannevig's (1919) experiments with eggs and larvae in waters of different salinities.

Salinity	Eggs	Larvae	Author
9.93	---	All die (34 hours)	Dannevig
12.47	High mortality	All die (52 hours)	Dannevig
18.71	Eggs survive	All die (138 hours)	Dannevig
22.36	Most suspended or sunk	Most sunk	Dahl
23.61	More than 1/2 float	1/2 float	Dahl
24.04	1/3 float	Most sunk	Dannevig
24.98	---	1/2 die (142 hours)	Dannevig
25.31	More than 1/2 float	1/2 float	Dannevig
26.10	All float	All Float	Dahl
27.85	All float	All float	Dannevig
29.99	---	All live (148 hours)	Dannevig
30.74	All live	---	Dannevig

Examination of the table reveals that both eggs and larvae are damaged by salinities below 13°/oo, but that eggs apparently can survive from about 19°/oo upward. This confirms the opinion (Anonymous 1932a) that eggs can stand a wide salinity range. Larvae, however, need a salinity over 25°/oo to survive for more than a few days. A. Dannevig's later work with Sivertsen (1933) disagrees somewhat, for they kept larvae in the laboratory at 22.41°/oo. With regard to flotation, below 23°/oo buoyancy is reduced for both eggs and larvae, while above 26°/oo all eggs and larvae float. All of these measurements apply to live fertilized eggs. Rognerud (1889) found that dead eggs did not float even in 37.32°/oo, and Hensen (1884) describes unfertilized eggs which floated in 18.5°/oo and began to sink at 17.2°/oo. There is a suggestion that these measurements apply only to European cod in the work of Ryder (1886) who claims 27.39°/oo fatally low for American cod eggs. And the question of how cod eggs and larvae survive in extremely low salinities of the inner Baltic seems unanswered.

However, the salinity of the water is not entirely determinative, either in the case of eggs or fry. Jacobsen and Johansen (1908) showed that cod eggs can change their specific gravity in a day or less to correspond to a salinity change of as much as 6°/oo, and Dahl (1909) points out that the position of the fry in the water may be varied by currents or even by the activity of the fish themselves.

There are many isolated observations on buoyancy and on the distribution of eggs and larvae in the ocean. Henly (1952) reports that cod larvae are buoyant in about 27.39°/oo, agreeing with Dahl's and A. Dannevig's work. Within and beyond the range of the table, eggs have been kept in 23.06°/oo to 27°/oo (Johansen and Krogh (1914), 31.86°/oo (Ryder 1886), 32.31°/oo (Bonnet 1939), and 31.11°/oo to 32.36°/oo (Carswell 1889). Hjort and Petersen (1905) found pelagic young cod in about 35°/oo. Larvae have been found in intermediate layers in the Baltic from 35 to 75 meters in 7.5°/oo to 14.2°/oo (Poulsen 1931), probably because of the abundance of food in these layers, although according to table 2 this salinity is dangerously low.

The net impression from the above is that the question of suitable and optimum ranges of salinity for eggs and larvae has not been settled. Laboratory experiments do not entirely confirm field observations, and there is a possible difference between American and European cod.

As A. Dannevig and Sivertsen (1933) point out, there may be a synergy between salinity and temperature. There is, of course, a physical relationship--sea water of a given salinity will decrease in density as temperature increases above 0°. But the effect on buoyancy is minor through the temperature and salinity ranges in which eggs and larvae are found. Below 10° and 35°/oo no temperature change can cause more than 0.001 change from the density at 0° (Knudsen 1901).

At the relatively shallow depths in which cod eggs and fry are found, the effects of pressure on density are so minute as to be negligible (Sverdrup, Johnson and Fleming 1942).

Miscellaneous

In addition to the effects of temperature and salinity on eggs and larvae, other factors have been noted and in some cases measured.

Water movements which may carry the eggs or young to areas not suitable for them can be important, as discussed by Johnstone (1906) and Fish (1929). Sund (1924) found that years in which there was less snow in Norway were years producing good year classes of cod. He postulates that the runoff in spring from heavy snows during the winter drives the fry-carrying bank water offshore to areas not suitable for the tiny fish.

Fish (1929) considered that storms might cause extensive damage to or destruction of eggs and larvae, and experiments by Rollefsen (1930) showed that cod eggs are indeed extremely susceptible to mechanical shock such as might be caused by storms or even surface waves caused by strong winds.

Poulsen (1931) found that cod larvae avoid water with an oxygen content of less than 4.9 $cm.^3$ per liter, much higher than Sundnes' (1957) critical value of 2.7 ml. per liter for mature fish.

A. Dannevig and Sivertsen (1933), in laboratory experiments, demonstrated that a pH of 4.1 was fatal to cod larvae, which survived in a range of pH 5.7 to pH 8.5.

Henly (1952) observes that after a certain stage of maturity the larvae must leave the surface water for hydrostatic balance, but that four meters depth was sufficient in a hatchery pond.

Schmidt (1931) concluded that some unknown factor in inshore water other than temperature and salinity has the effect of decreasing the average number of vertebrae in the cod.

FEEDING AND GROWTH

Temperature

It has been observed that cod in captivity grow about twice as much in July and August as they do in March and April, presumably due to the temperature difference (Anonymous 1935a). Dahl (1909) showed that the growth of cod fry is associated with temperature--that the fastest growth

seems to take place when temperatures are between 7° and 10°. Thompson (1943) concluded that the relatively fast growth and maturity of the North Sea and Baltic cod is due to the temperatures in these areas, which are higher than in the Northwest Atlantic, but this is not borne out in the case of the closely related haddock.

Growth is related to feeding and metabolism in general. With regard to feeding there may be two effects, the temperature in relation to the food organisms, as discussed by Hjort (1914), or temperature acting directly on the cod. Grenfell (1910) states that cod will not feed in water below 1.1°, and this is in fair agreement with McKenzie's findings that below this temperature they eat only sparingly. McKenzie (1934a, 1934c, 1935) kept records of the feeding of cod in tanks and concluded that temperature has marked effects, most feeding being done between 2.2° and 15.5°. In the high part of this range, a drop in temperature caused an increase in feeding, while in the lower part an advance in temperature did the same. Cod of all sizes fed rarely below 0°, but small cod fed up to 20°. In addition, the sizes of the pieces of food accepted varied with temperature changes by a factor as large as four, larger bites being taken in warmer water.

At the lower extremes it seems likely that the metabolic rate is affected. McKenzie notes (1935) that at -0.6° the fish swim very slowly and their respiratory rate is much reduced.

In further experiments published in 1938, McKenzie found that the fish actually seemed to have difficulty in swallowing when the temperature reached 1.1°, and that below this the cod apparently could not open their mouths to full gape.

In the natural environment, however, Lucas and Wimpenny (1953) found small cod feeding below 2°, although the optimum feeding temperature for small fish has been given as between 12° and 18° (Anonymous 1835a).

Schmidt (1929) speculated that the number of vertebrae, which increases as the water becomes cooler as mentioned above, might be related to the amount of food available rather than to the water temperature per se.

We are indebted primarily to McKenzie for our knowledge of the feeding habits of cod with respect to temperature. Summarizing his observations and bearing in mind the necessarily intimate relation between feeding and anabolism, we may conclude that cod feed regularly from about 2° to 15°. This is, of course, an oversimplification, because of the strong evidence that different sizes of cod have different optima within the general range, smaller fish tending to feed at higher temperatures.

But as McKenzie (1934c) points out, this range should be kept in mind when considering results from hook and line fishing as indications of abundance and distribution.

DISTRIBUTION AND ABUNDANCE OF MATURE FISH

Temperature

The effect of temperature on the distribution and abundance of the mature cod has long been a subject for study and also a matter of no little controversy. There have been those who would define "cod water" exclusively, Rodriguez M. and Rojo L. (1955), for instance, who say that on the Grand Bank it is water with temperatures from 2° to 4°, and Huntsman (1925) who cites 4.4° to 7.2°. But some authors (Anonymous 1935b, McKay 1934) have denied the existence of such an absolute entity.

Of particular interest is the West Greenland area, where cod were abundance from 1810 to 1823, then scarce until recent years when they have reappeared in enormous numbers. In the Disko Bay area, for example, cod were rare in the 1920's, but lately 30 percent of the total catch has been taken on the banks nearby. Tåning (1949, 1953) believes these changes are associated with warming of the waters in the early 19th century and again recently.

Lundbeck (1954) describes a change in distribution of cod in the Barents Sea which correlates with an increase in depth of the 0° layer. His rationale is that bottom areas which were formerly too cold have become habitable through this change.

Hjort seems to have been too restrictive when he wrote (1914) that the

occurrence of cod falls between the 6° and 8° (at 100 meters) isotherms all over the North Atlantic. Bigelow and Welsh (1925) say that 1.7° to 10.0° encompasses the range, although smaller fish may exceed the upper limit, while Jeffers (1931) gives 5° to 10° as the range.

Maslov (1944) considers that migrations of cod are influenced by hydrography, and Rollefsen (1949) states that mature cod seem to avoid low temperatures, although immature fish are less sensative.

Templeman and Fleming (1953) concluded that a study of eighty-one years of catch statistics could not demonstrate the association of the abundance of cod and temperature, probably because there were too many other variables. But McKenzie and Hachey (1939) found that for a relatively short period there was good correspondence between the catch of cod and the magnitude of the intermediate cold layer over the Scotian Shelf. Best landings occurred in years in which this layer was of minimum size.

Fishermen have fished by the thermometer, and in one case at least (McKenzie 1936), a government agency has addressed an open letter to fishing captains concerning the best temperature in which to catch cod.

There seems little doubt that cod are influenced by the temperature of the water they frequent and by the temperatures of adjoining bodies of water, but of late there has been a tendency to consider the temperature of the water in which feeding cod are found somewhat secondary to the food supply available (Ancellin 1955; Graham et al. 1954; Hachey, Hermann and Bailey 1954; Lee 1952; Rasmussen 1952, 1954a, 1954b, 1955; and Schroeder 1930). Of course, as expressed or implied, the presence and abundance of the food organisms may also depend on temperature conditions, but here the influence on the cod themselves is secondary.

McKenzie (1956), in reporting on several years of tagging experiments, relates that fish caught a day or so apart in the same area but in water of different temperatures showed different migration patterns--the inference being that different cod frequent different water.

Rasmussen (1952) maintains that West Greenland cod prefer to seek shallow water when forced away from the banks by low temperatures, but Hjort (1914) mentions a long standing theory, that in warmer years cod come closer inshore than usual.

And as a fragment of evidence that perhaps differential in temperature is important as it may also be in spawning, Templeman (1953b) found large cod numerous near the border of the below-zero intermediate cold layer.

To turn to observations for a specific area, on the Grand Bank good catches have been reported from -0.5° (Thompson 1936) to 7° (Thompson 1935). But usually the optimum is given as lying somewhere between 0° and 4° in spring (McKenzie 1936; Anonymous 1933, 1935b; Thompson 1935, 1936; Rodriguez M. and Rojo L. 1955; Rodriguez M. and Lopez C. 1954; Templeman 1954), with the lower half of this range being favored (McKenzie 1936, Anonymous 1935b, Thompson 1935).

In summer, 3° to 5° seems most favorable (McKenzie 1936, Anonymous 1935b, Rodriguez M. and Rojo L. 1955). Most authors agree that smaller cod are caught at higher temperatures both within and outside these ranges.

McKenzie (1936) says that on the Nova Scotia Banks in the spring -0.5° to 1.5° gives the best fishing, and that 3° is the upper limit. Others (Anonymous 1933, Thompson 1935) subscribe to this upper limit. In summer the picture is somewhat different. McKenzie cites 2.5° to 5.5°as the best temperature, and Ancellin's 1955 selection of a temperature over 1.9° agrees reasonably closely.

In the Gulf of St. Lawrence temperatures run higher, but a limiting value of 12° has been given (Anonymous 1935b). Thompson (1943) cites 0.5° to 6°, with 2° to 5° as the optimum. Huntsman (1925) gives a wide range of about 0.0° to 10.0°, but says that 4.4° to 7.2° is optimum. Tremblay, fishing experimentally with longlines (1942) found 8° most productive.

At West Greenland, in the pelagic long-line fishery at Holsteinborg Deep, 2.20° to 2.33° is given by Rasmussen (1954a, 1954b), but 3.1° to 4.0° has also been

cited (Anonymous 1953). The latter source also gives 1.6° to 4.0° for bottom long-lines, and Hachey, Hermann and Bailey (1954) agree that the West Greenland cod avoid temperatures below 1°.

In Labrador waters, cod prefer waters with temperatures from 1.7° to 5.6°, according to Grenfell (1910), although Templeman (1953a) reports the best catches on Hamilton Inlet Bank in the autumn from -0.93° to 1.23°. Whitely, Lindsay and Thompson (1932) say that above 3° is best and Rasmussen (1952) agrees that there is no profitable fishing below 2°.

In the Spitzbergen-Bear Island area on the eastern side of the Atlantic, Rasmussen (1952) and Lee (1952) state that fishing is not worthwhile below about 2°, and Lee elaborates that the general range is 3° to 5° in the summer and about 2° to 3° in winter, although pointing out that the fishing here is in different areas in the two seasons and may be on two different stocks of fish. Iversen (1934) concludes for the same area that cod usually do not frequent water masses below 0°.

Perhaps the best conclusion that can be reached was stated anonymously (1953b), that different groups of cod will live under and adapt to different temperatures, and that there is no one temperature suitable for cod wherever they are found.

Salinity and oxygen

Beaugé (1937) and Thompson (1943) have implied that cod are more abundant in water of a particular salinity range. But the general opinion seems to be that the abundance of cod in a particular area cannot be related to salinity (Anonymous 1933), although Poulsen (1944) speculates that migrations of mature cod in the Baltic may be related to salinity changes.

However, this seems reasonable when one examines the salinities in which cod have been found. Dambeck's report (1879) of cod living and spawning in a freshwater lake in Iceland seems extremely doubtful, but the occasional reports of cod straying upstream in rivers (Abbot 1871, Federsen 1880, Phillips 1883) probably are valid. Cod are found in low salinities in the Baltic, about 6°/oo, according to Poulsen (1931) and Alander (1952) and in full oceanic salinities elsewhere, about 35°/oo, (Damas 1909, Bigelow and Schroeder 1953, etc.). So under certain conditions at least, cod are found from nearly fresh water to full oceanic salinity.

There is considerable evidence that the distribution of cod in parts of the Baltic is related to the oxygen concentration (Jensen 1954, Alander 1951, Otterlind 1954). These authorities do not mention values, but Sundnes (1957) gives 2.7 ml. per liter as the critical value for cod and 0.80 as the value for asphyxia. Jensen (1952b, 1953, 1954) says that low oxygen concentrations may have caused the large numbers of deformed young cod found in the Baltic in certain years and the scarcity of mature cod in some areas. Alander (1951) and Otterlind (1954) agree.

MORTALITY

Temperature and other factors

In spite of the relatively great range of temperatures in which cod are naturally found and in which they can survive under artificial conditions, there are high and low limits to their temperature tolerance. The cod is a poikilotherm, with little or no internal temperature regulation, and Britton (1924) has shown that cod have temperatures less than 1° above that of their environment, at least in the range of ambient temperatures around 10°.

Lumby and Atkinson (1929) report the finding of dead codin otter-trawl catches in the North Sea in 1929 and conclude that a sudden drop in temperature was the cause. A. Dannevig (1947) reports that young cod in the littoral are sometimes killed by severe winters, but Hermann (1951) could not find a relation between cold years following the year of hatching in West Greenland and subsequent year class yields.

Bigelow and Welsh (1925) state simply that "freezing" is fatal. Carswell (1889) agrees and gives -1.7° as the freezing temperature. Templeman and Fleming (1956) claim that below -1.0° cod could be expected to die of cold, although Sleggs (1932) observes that scanty numbers of cod are found in nature at -1.6°. In older opinions, Earll (1880), Carswell (1889), and Nielsen

(1892), state that cod are killed in water of -1.1°. Contrast this with spawning reported at this temperature (Bigelow and Schroeder 1953). A. Dannevig (1930) says that at the Flødevig Hatchery cod have been held on occasion in water near -1° with only partial mortality.

McKenzie (1956) quotes a personal communication from A. H. Leim to the effect that a 52 centimeter cod in a tank evidenced no discomfort until the temperature reached -1.2°, although respiration ceased only slightly below this, at -1.5°, and heartbeat at -1.9°. Thompson (1943) reports that cod died when transferred from 0°, where they had apparently been doing well, to -0.6°. He considers that the lethal point lies close to -2°.

At the other extreme, McKenzie (1935) says that most of the large cod in tanks died when the temperature reached 15.0°, and that 20.0° was fatal to all large fish, although smaller ones survived.

Apparently the lethal temperatures for cod are somewhat variable, probably depending to a certain degree on what the fish have been conditioned to previously and how suddenly the temperature changes. But generally we may conclude that under appropriate circumstances some cod can survive from temperatures near the freezing point of sea water to 20.0°. Of particular interest are the relatively small variations in temperature near the freezing point which may cause large changes in behavior and death--v. Leim's cod which appeared comfortable and died of cold all within a range of 0.7°.

Sundnes (1957) reports that cod are asphyxiated when the oxygen content of the water is 0.80 ml. per l. or less.

RECAPITULATION

Cod are indeed influenced by the hydrographic conditions in the waters they frequent.

The maximum range of temperature for spawning is from below 0° to about 12°, with cod on European coasts spawning only over the lower half of this range. There is some evidence that cod leave the bottom and school pelagically to reproduce, and a suggestion that the thermocline is the preferred spawning habitat in some areas. Salinity seems to have very little influence on spawning.

Cod eggs can develop from below zero to about 14°, and the optimum temperature for the eggs and the larvae which hatch from them is probably from 5° to 7°. Eggs and larvae are subject to the effect of salinity change, with a critical point for survival perhaps in the neighborhood of 15°/oo, although there seems to be no natural upper limit. In many areas eggs and larvae are found in intermediate layers of water when surface salinities are not sufficient to cause them to float, that is, when they are below about 25°/oo. In the critical young stages, transport by currents and perhaps severe storms can be dangerous to the helpless eggs and nearly helpless larvae.

Cod growth varies with temperature; they grow more and apparently faster where the water is warmer. This is related to feeding, which takes place in roughly the full range which cod can endure, with smaller cod generally tending to feed more than the large at higher temperatures. It seems likely that reduced feeding at very low temperatures is related to metabolic function so that cod in very cold water actually cannot feed.

It does not seem possible to find a hard and fast definition of "cod water". This is perhaps because the distribution of feeding cod is more dependent on the distribution of the prey than it is on temperature per se. However, whatever the reason, larger fish are found in colder temperatures, and the optimum on the Grand Bank seems to be from 0° to about 5°, and on the Nova Scotian banks the optima are roughly the same. On the Labrador banks and the Gulf of St. Lawrence, the optima are slightly higher, as they are in the Spritzbergen-Bear Island area. Cod live in almost every salinity from nearly fresh water to full oceanic salinity about 35°/oo.

The internal temperature of the cod is similar to that of the ambient water, but in spite of this cod live in water of a wide range of temperatures, from nearly the freezing point to water considered comfortable for human bathing (20°). At

the low end of the range, cod seem to be skirting a dangerous margin, for a difference of only a fraction of a degree can mean the difference between thriving fish and dead fish. And actually, probably somewhat in the neighborhood of 15° is the upper limit for cod of appreciable size.

Bull (1936, 1938, 1952) established by experiments that cod can perceive changes in temperature of as little as 0.05° and of salinity as small as 0.17°/oo. Since his findings in these experiments show results for cod very similar to those for other teleosts, we may extrapolate from another experiment in which cod were not tested and assume that cod can detect differences in pH on the order of 0.05.

We may conclude as Jensen (1952a) did, that much valuable work has been done, but that much remains to be done in the future.

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